Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

Number 61 May 10, 1962 New Haven, Conn.

THE AFFINITIES OF THE PINK-HEADED DUCK (*RHODONESSA CARYOPHYLLACEA*)

PHILIP S. HUMPHREY AND S. DILLON RIPLEY

The rare or extinct Pink-headed Duck of India has had a checkered taxonomic history, having been placed at one time or another with the perching ducks (Cairinini), the dabbling ducks (Anatini), and the pochards (Aythyini). Delacour and Mayr (1945:23-24) in their brilliant revision of the family Anatidae considered *Rhodonessa* as belonging to the tribe Anatini because of similarities in display and posture. Later, Delacour (1956:197) stated that it "is probably related to *Anas* more nearly than to any others, but it may also have some connection with the pochards, as it somewhat approximates in proportions the species of *Netta*, and it has a similar trachea. It certainly shows no close relationship to the Wood Ducks (Cairinini)." Verheyen (1955:22) places *Rhodonessa* with the pochards, an alliance which had been suggested earlier by Garrod (1875:153-154) on the basis of the trachea. Peters (1931:170) put *Rhodonessa* between *Malacorhynchus* (Pink-eared Duck) and *Aix* (Wood Duck) in his subfamily Anatinae, which also included the dabbling ducks and a variety of other forms. Phillips (1922:90-93) and Salvadori (1895:61-63) placed the genus in a subfamily Plectropterinae among genera which are now considered to be perching ducks (Cairinini).

Most recently Johnsgard (1961:78,80) has recognized the aythyine affinities of *Rhodonessa;* he considers *Rhodonessa* a connecting link (along with *Marmaronetta*) between the Aythyini and the Anatini. Woolfenden (1961:114), using several osteological features as evidence, has placed *Rhodonessa* in the tribe Aythyini.

Rhodonessa has had an uncertain status because it combines some of the characters of two very different groups of waterfowl: the pochards on the one hand, and on the other, ducks which are better adapted for a more terrestrial existence, namely the dabbling ducks and perching ducks. This combination of characters has led some workers to suggest that the Pink-headed Duck might be a "link" relating in a phylogenetic sense the pochards and the dabbling ducks.

Humphrey's interest in this problem was aroused when it was noted that the trachea of the male Pink-headed Duck is very similar to tracheae of males of species in the tribe Aythyini, differing from these only in small details. This striking morphological similarity and Ripley's interest in the curious distribution of *Rhodonessa* and other Indian birds have prompted us to investigate further the affinities of this puzzling genus.

ACKNOWLEDGMENTS

Humphrey's part of this study was supported by the National Science Foundation as part of a project on the anatomy of the trachea of ducks and the classification of that group.

Anatomical specimens examined during the course of this study were obtained through the generosity of M. C. Downes (Department of Fisheries and Game, Australia), H. J. Frith (Wildlife Survey Section, C.S.I.R.O., Australia), R. P. Grossenheider, G. S. Hunt, G. V. T. Matthews (The Severn Wildfowl Trust), K. C. Parkes, W. H. Partridge, Peter Stettenheim, the Departments of Conservation of the states of Michigan and Washington, the Department of Animal Pathology (Cambridge, England), and the University of Washington Marine Biological Station at Friday Harbor; this study would not have been possible without the invaluable help of these people and institutions. We are indebted to the British Museum of Natural History, the American Museum of Natural History,

the United States National Museum and the University of Michigan Museum of Zoology for the use of specimens in their care. Many of the specimens examined during the course of this study were first obtained while Humphrey was at the University of Michigan Museum of Zoology; we are especially grateful to R. W. Storer and the late Josselyn Van Tyne for allowing this material to be incorporated in the collections of the Yale Peabody Museum of Natural History.

Our thanks must also go to Mrs. Shirley Hartman for preparing the illustrations and to Mr. George E. Watson for many helpful suggestions.

STRUCTURAL FEATURES

Little is known of the anatomy of the Pink-headed Duck. Garrod (1875:153-154) described and figured the trachea and syrinx of both sexes; Verheyen (1955:22) and more recently Woolfenden (1961:14, 41, 52, 54, 114) have commented on the osteology of the species.

Plumage pattern and general appearance. The Pink-headed Duck was a long-necked, rather awkward looking bird and at first sight, little like a pochard in bodily proportions. The posture of the species and its display habits (discussed below) have led some authors, notably Delacour and Mayr (1945), to ally it with the dabbling ducks.

A general comparison of the plumage patterns of the Pink-headed Duck and all other waterfowl leaves us with the impression that the species has in this character more in common with the pochards than with any other group. The coloration of the Pink-headed Duck (apart from the pink head and neck, which are in color unique among waterfowl) is very much like that of the pochards. The similarity is especially noteworthy in the pattern of coloration of the wing (Ripley, 1950:903-904). *Rhodonessa* lacks an iridescent speculum, and in fact has secondaries which are practically identical in markings with those of many pochards.

Trachea. The trachea of the male Pink-headed Duck is in its general features indistinguishable from the tracheae of males of the tribe Aythyini. However, it differs in the ag-

gregate of several details of structure from the tracheae of males of any of the pochards.

We have examined specimens or figures of tracheae of males of all species in the tribe Aythyini except *Netta erythrophthalma*, *Aythya nyroca*, and *Aythya novae-seelandiae*.

Through the courtesy of Dr. James D. McDonald of the British Museum of Natural History we have been able to study a specimen of the caudal part of the trachea of a male Pink-headed Duck. Males of *Rhodonessa* and the various species of Aythyini are alike in general conformation of the syringeal region. The similarity is most striking in 1) the form of the partly bony, partly membranous swelling or dilatation to the left, and 2) the conformation of the laterally expanded, partly fused rings anterior to the tracheo-bronchial junction (Figure 1).

In form of the dilatation to the left, male *Rhodonessa* differs from males of the tribe Aythyini as follows:

1) the membrane-covered fenestrae are poorly developed.

2) the dilatation is not as strongly laterally compressed as in the Aythyini.

3) the dilatation does not extend as far anteriorly (cephalad) as in the Aythyini.

4) the lateral plane of orientation of the dilatation is dorsal to ventral not dorso-medial to ventro-lateral as in the Aythyini.

5) the dilatation is more expanded or swollen caudally than in the Aythyini.

In every respect save the last, the dilatation of the caudal end of the trachea of *Rhodonessa* is less well developed than in the Aythyini. In *Rhodonessa* this dilatation is clearly a somewhat less elaborate version of the same structure in the Aythyini. *Rhodonessa* resembles no other group of ducks in this respect.

According to Garrod (1875:154), the trachea of the male Pink-headed Duck has "a slight fusiform dilatation" anterior to the syringeal region. Mid-tracheal swellings of one kind or another occur commonly in only two of the major groups of waterfowl, the Mergini (*Bucephala*, *Mergus*, *Histrionicus*, *Melanitta*) and the Aythyini (several species of *Aythya*,

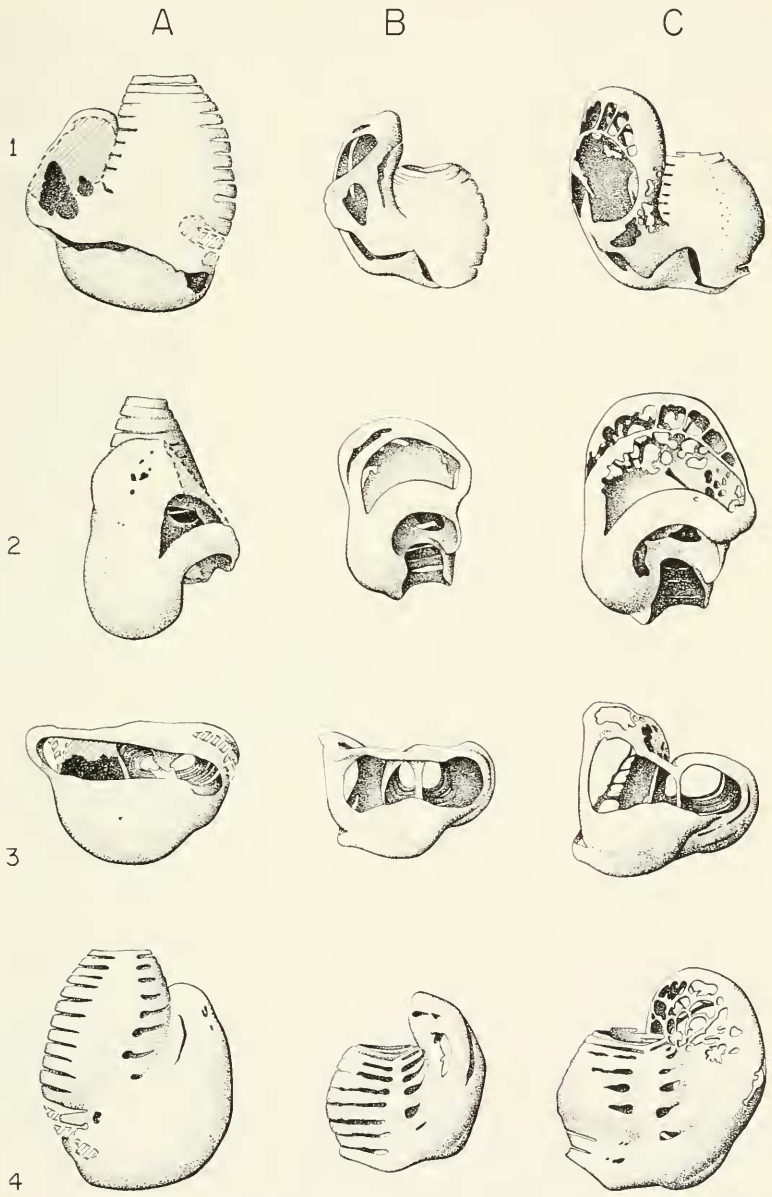

Figure 1. Caudal ends of tracheae of males of A) *Rhodonessa caryophyllacea,* B) *Metopiana peposaca,* and C) *Aythya affinis;* each specimen drawn in the following views: 1) dorsal, 2) left lateral, 3) caudal, and 4) ventral. Magnification x 1.18.

Netta). One, and possibly more, species of *Anas* (*Anas versicolor*, but not all species are known anatomically) have a mid-tracheal swelling.

Garrod (1875:154) describes the caudal end of the trachea just anterior to the syringeal region of the male Pink-headed Duck as follows: "the lower end of the trachea is hardly contracted at all. There is, however, a slight thinning of the anterior portions of some of the inferior tracheal rings. . . . a small, transverse, anterior fenestra being the result." Garrod's figure of the trachea of the male of this species illustrates 13 such fenestrae. A similar modification of the ventral parts of some of the more caudal tracheal rings occurs in male *Clangula* (tribe Mergini), but there are in that species only seven fenestrae. Males and females of *Sarkidiornis* (Cairinini) have fenestrae of this kind in the caudal part of the trachea; these fenestrae are fewer and less well developed in the females.

The structure of the syringeal region of the tracheae of males of the genera *Aythya*, *Netta*, and *Metopiana* is peculiar to the group. From the standpoint of the structure of the male syrinx, *Rhodonessa* clearly belongs in the tribe Aythyini. The syringes of males of the tribes Anatini and Cairinini have much in common structurally and differ significantly from those of *Rhodonessa*, *Aythya*, *Netta*, and *Metopiana*.

Humerus. Woolfenden (1959:184) has described a method of distinguishing "the humeri of the Anatinae from those of the Aythyinae [classification of Peters, 1931], based on certain characters of the pneumatic fossa . . . . In the Anatinae the fossa is deeper and partially excavates the medial bar. The construction is such that the palmar surface of the bar is not completely visible. Furthermore, the fossa usually possesses many bony struts. In the Aythyinae the pneumatic fossa is shallower, and the medial bar is essentially continuous with the shaft, exposing its palmar surface. Struts within the fossa are rare; in most cases the wall is solid."

Woolfenden found that the pneumatic fossa of *Metopiana peposaca* agrees "in all respects with those of the Anatinae." He says further that "this deviation from what seems a reliable method of distinguishing the two subfamilies may be of phylo-

gentic significance, for Delacour and Mayr (1945:25-26) consider *Metopiana*, along with *Netta rufina* and *Aythya erythrophthalma*, to 'constitute a bridge between the river ducks and the more specialized pochards of the genus *Aythya* . . . .'"

We have examined the pneumatic fossa of the humerus of *Anas platyrhynchos*, *A. fulvigula*, *A. falcata*, *A. poecilorhyncha*, *Aythya marila*, *A. fuligula*, *A. ferina*, *Metopiana peposaca*,

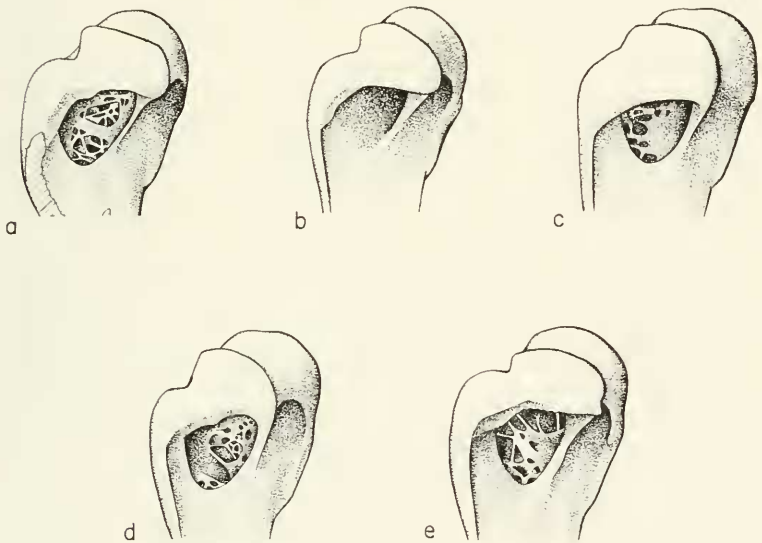

Figure 2. Head of left humerus, anconal view; a) *Rhodonessa caryophyllacea*, b) *Aythya marila*, c) *Metopiana peposaca*, d) *Mergus serrator*, and e) *Anas platyrhynchos*. Magnification x 1.75.

Rhodonessa caryophyllacea, *Histrionicus histrionicus*, *Melanitta fusca*, *M. nigra*, *Somateria mollissima*, *Bucephala albeola*, *Mergus serrator*, *M. merganser*, and *Aix sponsa*. Using Woolfenden's criterion for classifying pneumatic fossae into "aythyine" or "anatine" types, we find the following:

"Anatine" pneumatic fossa: *Anas*, *Metopiana*, *Rhodonessa*, *Mergus*, *Aix*. (Figure 2.)

"Aythyine" pneumatic fossa: *Aythya*, *Bucephala*, *Histrionicus*, *Melanitta*, *Somateria*.

The fact that *Mergus* has an "anatine" pneumatic fossa suggests to us that this character has undoubtedly arisen independently in three or more different groups (Mergini, Aythyini, Anatini). Delacour and Mayr (1945) have pointed out the close relationship between *Bucephala* and *Mergus;* Humphrey (1955) has shown that *Mergus* probably evolved from a *Bucephala*-like ancestor. We feel that the "aythyine" pneumatic fossa of *Bucephala* is evidence that the "anatine" pneumatic fossa of *Mergus* is a derived condition which in no way indicates relationships with the tribe Anatini. Therefore, the *Anas*-like condition of the pneumatic fossa of *Metopiana* does not necessarily indicate that this genus has any close affinity to the Anatini. In view of the foregoing, the "anatine" condition of the pneumatic fossa of *Rhodonessa* cannot be used as evidence to clarify the relationships of this genus.

Feet. The feet of the Pink-headed Duck have a number of characters in common with those of *Anas*, e.g., lack of a lobe on the hallux, digits III and IV approximately equal in length or digit III slightly longer, digits relatively short compared to length of humerus. However, there are some features of the foot of *Rhodonessa* which suggest that its resemblance to the feet of dabbling ducks is secondarily derived.

The fact that the Pink-headed Duck, by its tracheal anatomy obviously a pochard, has feet like a dabbling duck prompted us to compare the feet of dabbling ducks and pochards. To this end we measured skeletal elements of the feet of the following species:

Anas discors ♂
" *acuta* ♂
" *querquedula* ♀
" *gibberifrons* ♂
" *cyanoptera* ♂
" *rubripes* 10 ♂
Aythya marila ♂
" *fuligula* ♂
" *nyroca* ♀
Aythya collaris ♂
" *americana* ♂
" *ferina* ♀
" *valisineria* ♂
" *affinis* 8 ♂
Metopiana peposaca ♂
Netta rufina
Rhodonessa caryophyllacea ♀

Measurements of these specimens are presented in Table 1 which also includes means, standard deviations, minima and maxima of the measurements of samples of *Anas rubripes* and *Aythya affinis*.

As is apparent from examination of specimens of dabbling ducks (*Anas*) and pochards (*Aythya*), these two groups of waterfowl differ in size of foot, the pochards having relatively much larger feet than the dabbling ducks. Using greatest length of humerus as an index of general body size, the greatest length of the tarsometatarsus and of each digit (minus ungual phalanx) was expressed as a per cent of humerus length. These ratios are presented in Table 2 where it can be seen that in every case except length of tarsometatarsus the ratios of the elements of the foot of *Rhodonessa* are much smaller than those of *Aythya* and fall among those of the *Anas* group. The tarsometatarsus of *Rhodonessa* is relatively somewhat shorter than that of any dabbling duck but rather long for a pochard, although those of some pochards (*Aythya nyroca*, *A. valisineria*, *Metopiana*) are about the same relative length or slightly longer. In common with the dabbling ducks and *Rhodonessa*, *Metopiana* has relatively short digits; except for the hallux, the digits of *Netta rufina* are also very short. The relative length of the tarsometatarsus of *Netta* is short like that of the more typical pochards.

Possibly there is a difference in the relative lengths of the humeri of dabbling ducks and pochards correlated with differences in the flying abilities of the two groups. Although we know of no way of testing for this possibility, we doubt that there is enough of an adaptive difference in relative length of the humerus in the two groups to invalidate using length of this element as a measure of body size and as a means of comparing the relative lengths of the elements of the foot.

There is a clear cut difference between the species of *Anas* and those of *Aythya* in the relative lengths of digits III and IV. In *Aythya* (and *Netta rufina*) digit IV is longer than digit III (see Table 3). In *Anas* digit III is usually longer but may be equal to or slightly shorter than digit IV. In *Anas rubripes* (sample of ten males) digit IV is usually slightly shorter (up to 3.6 per cent shorter) than digit III; in five out of ten speci-

Table 1

Measurements in (millimeters) of skeletal elements of feet of *Netta rufina, Metopiana peposaca, Rhodonessa caryophyllacea,* and various species of *Anas* and *Aythya*. One specimen of each species measured except as indicated below.

1. Mean and standard deviation of samples of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of samples of 8 males.

	Digit II		*Digit III*			*Digit IV*	
	IIp	*IId*	*IIIp*	*IIIz*	*IIId*	*IVp*	*IVz*
Anas							
discors ♂	14.4	10.6	14.8	10.8	8.8	12.1	8.2
acuta ♂	20.7	16.1	21.7	15.0	13.1	16.9	12.0
querquedula ♀	14.3	11.3	14.7	10.2	8.8	12.0	7.8
gibberifrons ♂	17.4	13.4	17.9	12.1	11.4	14.4	9.7
cyanoptera ♂	16.2	12.7	16.5	12.3	10.2	13.5	9.3
rubripes[1]	22.4 ± 0.2	16.7 ± 0.6	22.8 ± 0.7	15.5 ± 0.4	13.1 ± 0.4	18.2 ± 0.5	12.4 ± 0.5
rubripes[2]	23.7	17.7	24.0	16.2	13.7	19.0	13.3
rubripes[3]	21.2	15.9	21.9	14.9	12.5	17.2	11.7
Aythya							
marila ♂	26.2	18.6	25.7	18.8	15.7	20.7	15.7
fuligula ♂	22.8	17.0	22.2	16.1	14.0	18.5	13.3
nyroca ♀	20.7	15.8	21.1	15.5	13.2	17.5	12.5
collaris ♂	23.2	17.3	23.0	16.8	14.5	19.1	14.2
americana ♂	26.2	19.2	25.0	18.1	15.7	20.4	15.5
ferina ♀	25.2	18.6	25.0	18.1	15.0	20.0	14.3
valisineria ♂	29.6	22.2	28.6	20.8	17.3	23.9	16.9
affinis[4]	23.4 ± 1.1	17.3 ± 1.1	22.7 ± 1.2	16.2 ± 1.0	13.9 ± 1.0	18.9 ± 0.9	13.7 ± 0.8
affinis[2]	24.6	18.6	23.8	17.1	15.0	20.0	14.3
affinis[3]	20.9	14.9	20.0	13.8	11.7	16.8	11.8
Netta							
rufina ♀	25.2	19.2	24.5	17.9	16.0	19.9	14.3
Metopiana							
peposaca ♂	24.7	18.0	24.0	17.5	14.6	19.5	13.9
Rhodonessa							
caryophyllacea ♀	23.0	16.6	23.1	15.7	12.9	18.5	12.3

TABLE 1 (Continued)

Measurements in (millimeters) of skeletal elements of feet of *Netta rufina, Metopiana peposaca, Rhodonessa caryophyllacea,* and various species of *Anas* and *Aythya*. One specimen of each species measured except as indicated below.

1. Mean and standard deviation of samples of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of samples of 8 males.

	Digit IV		*Digit I*	*Digit II*	*Digit III*	*Digit IV*	*Tarsometatarsus*
	IV3	*IVd*					
Anas							
discors ♂	6.4	6.7	6.4	25.0	34.4	33.4	31.2
acuta ♂	9.0	11.3	10.5	36.8	49.8	49.2	45.5
querquedula ♀	5.9	7.0	6.9	25.6	33.7	32.7	31.0
gibberifrons ♂	7.5	9.1	8.3	30.8	41.4	40.7	36.5
cyanoptera ♂	7.5	8.5	7.5	28.9	39.0	38.8	34.6
rubripes[1]	9.6 ± 0.4	10.6 ± 0.4	10.3 ± 0.5	39.1 ± 1.3	51.3 ± 1.3	50.7 ± 1.6	46.9 ± 1.2
rubripes[2]	10.4	11.5	11.0	41.0	53.9	53.8	49.0
rubripes[3]	9.0	9.9	9.7	37.1	49.6	48.2	44.8
Aythya							
marila ♂	13.0	13.5	14.4	44.8	60.2	62.9	38.9
fuligula ♂	11.4	12.4	11.6	39.8	52.3	55.6	33.3
nyroca ♀	10.7	11.4	10.2	36.5	49.8	52.1	33.5
collaris ♂	12.1	12.5	11.1	40.5	54.3	57.9	34.7
americana ♂	12.9	13.2	12.8	45.4	58.8	62.0	39.3
ferina ♀	12.2	12.7	13.5	43.8	58.1	59.2	37.7
valisineria ♂	15.2	15.2	14.3	51.8	66.7	71.2	45.0
affinis[4]	11.3 ± 0.7	12.5 ± 1.0	12.6 ± 1.0	40.7 ± 2.2	52.7 ± 3.2	56.3 ± 3.3	35.4 ± 0.9
affinis[2]	11.8	13.8	13.6	43.2	55.9	59.3	36.7
affinis[3]	9.6	10.5	11.2	35.8	45.5	48.7	20.9
Netta							
rufina ♀	12.0	13.3	14.6	44.4	58.4	59.5	43.7
Metopiana							
peposaca ♂	11.1	12.1	12.1	42.7	56.1	56.6	45.6
Rhodonessa							
caryophyllacea ♀	9.7	11.0	11.5	39.6	51.7	51.5	45.7

mens, digit IV was about the same length as or slightly longer (up to 1.4 per cent longer) than digit III.

Rhodonessa is *Anas*-like in this character: digit IV is 0.9 to 2.1 per cent (three specimens) shorter than digit III.

We have compared the relative lengths of the phalanges of the feet of *Rhodonessa*, *Netta*, *Metopiana*, and the various species of *Anas* and *Aythya* using the proximal phalanx of digit III as the basis for the intramembral proportions. The relative lengths of the phalanges of *Rhodonessa* as compared with those of the pochards and the dabbling ducks lead us to believe that the dabbling-duck-like foot of *Rhodonessa* has evolved from a typical pochard foot. Unfortunately, lack of material makes it impossible to analyze the variability of the relative lengths of the phalanges of *Rhodonessa*. We suspect, however, that the variability is of the same order of magnitude as found in a sample of eight *Aythya affinis*. If this is true, we see no other explanation for the peculiar phalangeal proportions of the foot of *Rhodonessa* than that they are the result of modification of an ancestral pochard-like foot.

The relative length of the proximal phalanx of digit II of *Rhodonessa* is greater than the maximum found for *Anas* and well within the minimum range for *Aythya*. Allowing for variability, one could safely say that this element is on the large side for *Anas* or on the small side for *Aythya*. The distal phalanx of digit II of *Rhodonessa* is relatively rather short for either *Anas* or *Aythya*. In digit III of *Rhodonessa* the second phalanx is relatively shorter than in any of the eight pochards studied and is slightly below the average of the six dabbling ducks. The distal phalanx is relatively smaller than the smallest of *Anas* and much smaller than in *Aythya*. The hallux (digit I) of *Rhodonessa* is relatively longer than in *Anas* and among the shorter of *Aythya*. (See Table 4.)

In summary, the foot of *Rhodonessa* is *Anas*-like in 1) the relative shortness of digits II, III and IV, 2) the absence of a lobe on the hallux and 3) the relative lengths of digits III and IV; it is more pochard-like (but perhaps intermediate) in 1) length of tarsometatarsus and 2) length of hallux. The intramembral proportions of the foot of *Rhodonessa* suggest that the phalanges have undergone in evolution a differential

Table 2

Lengths of digits and tarsometatarsus expressed as per cent of length of humerus.

1. Mean and standard deviation of ratios from sample of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of ratios from sample of 8 males.

	Digit I	*Digit II*	*Digit III*	*Digit IV*	*Tarsometatarsus*
Anas					
discors ♂	10.1	39.4	54.3	49.2	49.3
acuta ♂	11.4	39.8	54.0	49.3	49.3
querquedula ♀	10.5	39.0	54.3	49.8	47.2
gibberifrons ♂	11.8	43.9	58.9	58.0	52.0
cyanoptera ♂	11.4	44.0	59.5	59.1	52.7
rubripes[1]	10.8 ± 0.5	44.0 ± 1.1	53.9 ± 1.3	53.0 ± 1.6	49.3 ± 0.7
rubripes[2]	11.6	43.0	56.6	56.5	50.2
rubripes[3]	9.9	39.4	52.2	51.1	48.0
Aythya					
marila ♂	16.4	51.0	68.6	71.5	44.4
fuligula ♂	14.8	51.0	67.9	71.2	42.5
nyroca ♀	14.1	50.5	69.0	72.2	46.4
collaris ♂	14.6	53.1	71.2	75.9	45.5
americana ♂	14.1	50.0	64.8	68.3	43.3
ferina ♀	15.9	51.7	68.6	70.0	44.5
valisineria ♂	15.2	55.0	70.9	75.5	47.8
affinis[4]	15.7 ± 1.2	50.9 ± 2.6	65.9 ± 3.6	70.3 ± 3.8	44.3 ± 0.9
affinis[2]	17.1	53.0	68.5	72.6	45.2
affinis[3]	14.2	45.2	57.5	61.5	42.7
Netta					
rufina ♀	14.2	43.1	56.8	57.9	42.5
Metopiana					
peposaca ♂	12.5	44.1	58.0	58.6	47.2
Rhodonessa					
caryophyllacea ♀	11.7	40.3	52.6	52.4	46.5

Table 3

Comparison of lengths of digts III and IV. The differences in the lengths of digits III and IV are listed; in the adjacent columns these differences are expressed as per cent of the length of digit III. *Aythya affinis:* of 8 specimens (males) digit IV was always longer by 5.6 per cent to 8.2 per cent. *Anas rubripes:* of 10 specimens (males) digit III was longer than digit IV in 7 individuals and shorter than digit IV in 3 individuals.

1. Mean of sample of 7 males.
2. Minimum.
3. Maximum.
4. Mean of sample of 8 males.
5. Mean of sample of 3 males.

	Digit III longer than Digit IV			*Digit III longer than Digit IV*	
	III-IV	$\frac{(III-IV) \times 100}{III}$		*IV-III*	$\frac{(IV-III) \times 100}{III}$
Anas		*per cent*	Aythya		*per cent*
discors	1.0	2.9	marila	2.7	4.5
acuta	0.6	1.2	fuligula	3.3	6.3
querquedula	1.0	3.0	nyroca	2.3	4.6
gibberifrons	0.7	1.7	collaris	3.6	6.6
cyanoptera	0.2	0.5	americana	3.2	5.5
rubripes[1]	1.0	1.9	ferina	1.1	1.9
rubripes[2]	0.1	0.2	valisineria	4.5	6.8
rubripes[3]	1.9	3.6	affinis[4]	3.6	6.8
Rhodonessa			affinis[2]	3.0	5.6
caryophyllaeca	0.2	0.9	affinis[3]	4.3	8.2
			Netta		
			rufina	1.1	1.9
			Metopiana		
			peposaca	0.5	0.9
			Anas		
			rubripes[5]	0.4	0.8
			rubripes[2]	0.2	0.4
			rubripes[3]	0.7	1.4

TABLE 4

Lengths of phalanges expressed as per cent of the length of the proximal phalanx of digit III.

1. Mean and standard deviation of ratios from sample of 10 males.
2. Maximum.
3. Minimum.
4. Mean and standard deviation of ratios from samples of 8 males.

	Digit II		*Digit III*		*Digit IV*			
	IIp	*IId*	*IIIp*	*IIId*	*IVp*	*IVp*	*IVp*	*IVd*
Anas								
discors ♂	97.4	71.6	73.0	59.5	81.8	55.4	43.2	45.3
acuta ♂	95.5	74.2	69.2	60.4	78.0	55.1	41.5	52.1
querquedula ♀	97.3	76.9	69.4	59.8	81.6	53.1	40.1	47.6
gibberifrons ♂	97.2	74.9	67.6	63.7	80.5	54.1	44.9	50.8
cyanoptera ♂	98.3	77.0	74.5	61.9	81.8	56.4	45.5	51.5
rubripes[1]	98.5 ± 1.6	73.4 ± 2.0	67.9 ± 0.9	57.4 ± 1.8	79.8 ± 1.2	54.5 ± 1.3	42.2 ± 1.7	46.4 ± 1.6
rubripes[2]	101.3	76.6	69.6	60.0	81.4	56.8	44.7	49.1
rubripes[3]	96.5	70.9	66.5	54.4	78.0	52.8	39.6	44.5
Aythya								
marila ♂	104.0	72.4	73.1	61.1	80.5	61.1	50.6	52.5
fuligula ♂	102.8	76.5	72.5	63.1	83.3	59.9	51.4	55.9
nyroca ♀	98.2	74.9	73.5	62.6	83.0	59.3	50.7	54.0
collaris ♂	100.9	75.2	73.0	63.0	83.0	61.8	52.6	54.4
americana ♂	104.8	76.8	72.4	62.8	81.6	62.0	51.6	52.8
ferina ♀	100.8	74.4	72.4	60.0	80.0	57.2	48.8	50.8
valisineria ♂	103.5	77.6	72.7	60.5	83.6	59.1	53.2	53.2
affinis[4]	103.1 ± 1.5	76.1 ± 1.4	71.1 ± 1.1	61.0 ± 1.6	83.1 ± 1.1	60.2 ± 0.7	49.7 ± 1.2	55.0 ± 2.0
affinis[2]	104.9	78.2	72.6	63.0	84.4	61.4	51.5	58.0
affinis[3]	100.5	74.5	69.0	58.5	81.5	59.0	48.0	52.5
Netta								
rufina ♀	102.9	78.4	73.1	65.4	81.3	58.4	49.0	54.3
Metopiana								
peposaca ♂	103.0	75.0	73.0	60.8	81.3	57.9	46.2	50.4
Rhodonessa								
caryophyllacea ♀	99.6	71.9	68.0	55.9	80.1	53.3	42.0	47.6

reduction, the more proximal phalanges being least affected and the distal phalanges most affected. This is most apparent in digit III but is suggested in digit II. Digit IV must have undergone the greatest reduction of all from the presumed ancestral pochard condition of having been longer than digit III. Miller (1937:45) found in his studies of the feet of geese that "increase or decrease in toe length takes place to a greater degree in digits two and four than in three, and increase or decrease in phalangeal length takes place to a greater degree in distal (exclusive of ungual) than in proximal phalanges."

BEHAVIOR AND ECOLOGY

There has been little recorded about *Rhodonessa* beyond the fact that it has always been observed uncommonly. The Pink-headed Duck appears to have been a solitary species, occurring as pairs in the breeding season or small groups in winter (Hume and Marshall, 1881, 3:176) on isolated marshy ponds or swampy lakes and not joining the large wintering concentrations of migrant waterfowl. Delacour (1956:198) notes that its behavior was much like that of dabbling ducks. The species nested in April in long grass (*Andropogon*) or grass tufts sometimes away from the water. The eggs were white and uniquely spherical (Finn, 1909:25) and the nests well-formed with no special lining.

The male had a whizzy whistle like a Mallard but lower and weaker. The female had a low quack. Finn (1909:86), however, speaks of the male's call as quite unlike that of any other duck, resembling the syllables "wugh-ah."

Males when together (in captivity) were noted to display like Mallards but more simply. The head was drawn in between the shoulders while the head feathers were puffed out. Following this the neck was stretched upwards and the call uttered. However, as Delacour (1956:198) has observed and described the display, it was so simple that it lacks any real relationship to the display of a dabbling duck. It resembled equally well the simplest forms of aythyine display such as that of *Metopiana* for example, lacking only the angular position of the bill pointed upwards at the climax of the neck-stretch. These

observations, in captivity, may have been of birds insufficiently stimulated to have produced a diagnostic display.

Flight of *Rhodonessa* is said to have been light and easy and the habits like those of a true surface-feeder (Finn, 1909: 86). Finn (1915:25) observed an individual dive "as neatly and long as a pochard." Perching was never observed.

The Pink-headed Duck was a solitary, non-migratory species which was local in distribution; the center of its restricted distribution was the Gangetic area of the "terai" of northern Bihar. The last record of its occurrence in nature was in 1935 (C. M. Inglis). Jerdon (in Hume and Marshall, 1881, 3:176) reports that the birds remained out in the center of the pond during the day and so presumably fed at night. Shillingford (in Hume and Marshall) reports that a gizzard contained water weeds and small shells. The duck was said not to have been a palatable species, indicating an animal diet.

It is unfortunate that so little is known of the habits and behavior of the Pink-headed Duck. The lack of information is particularly aggravating considering that this now extinct or nearly extinct species was at one time not uncommon in collections of European aviculturists where it displayed but never nested. All that can now be said is that the anatomy and proportions of the foot of *Rhodonessa* indicate feeding and locomotor adaptations very much like those of dabbling ducks. The sparse behavioral information available provides some if not overwhelming support for this notion.

DISCUSSION

What sort of history of ecological changes can have produced the Pink-headed Duck, a pochard with strikingly anatine modifications of the foot? The most likely sorts of environmental changes would have involved a shift from the more typical pochard habitat, that is, a marine or inland sea littoral environment, to the present one of marshy, fresh water ponds. It appears that just such a change took place in India during Tertiary times.

The Neogene period, characterized by a general regression in the middle Miocene, brought an isolation of the eastern

Mediterranean into an inland sea. This eastern Mediterranean province is described by Gignoux (1955:554-5, 587-8, fig. 144). Characteristically beginning with the upper Vindobonian or upper Sarmatian, the inland sea thus formed began to show isolated genera of invertebrates responsive to decreased salinity with the outpourings of large fresh water rivers. The easternmost of these lacustrine basins is the Aral-Caspian which stretched north to Samara and east far beyond the Aral Sea. This eastern basin escaped the reinvasion of the Mediterranean which occurred in the Quaternary with the opening of the Dardanelles and the extinguishing of the Levantine and western Caspian faunas.

The southern parts of this area of trapped inland sea in the southern Caspian and south of the newly risen Caucasus represent part of the old Mesogean or Tethys Sea basin, continuous through to the Indian Ocean and cut at the beginning of the Miocene.

Similarly in India, the Miocene system (Wadia, 1944:256-275) shows a series of clays and sandstones whose characters suggest deposition in an estuary or the broad mouth of a river (Gaj Series in Sind). This shows a regression of the sea border and its replacement by the wide basin of an estuary. A good example of this sequence is the Potwar trough which shows deposits of nummulitic form over Mesozoic rocks, overlain by brackish-water sediments of Aquitanian and Burdigalian age (=lower Oligocene and upper Miocene) followed by the fluviatile and sub-aerial Siwalik strata.

How far southward the Siwalik system lies is unclear; much of it is probably buried under the recent alluvium of the Ganges. Siwalik birds are interesting in that *Phalacrocorax*, *Pelecanus*, and *Mergus* are represented, genera found in India today, and characteristic of very large lakes or large river systems.

The Pleistocene system in India reveals evidences of glaciation in the form of moraines and polished and grooved rock at low altitudes in the Himalayas, and also the desiccation of the Tibetan lakes consequent on the disappearance comparatively recently of the glaciers of the ice age.

The plains of India north of the peninsula reveal another aspect of the Pleistocene in the Indo-Gangetic depression filled

with thousands of feet of alluvium (Wadia, 1944, fig. 33). The present river systems bear little relation to their past history even during historic times. This is a vast area of wandering rivers and repeated alterations of clays, sand and marls with recurring layers of peat, lignite and some forest beds. Huge deltaic areas as in Bengal cover parts of the former Bay of Bengal, or in the west, as in the Rann of Kutch, remains of bays of the Arabian Sea.

All of this intervening plain except for occasional projections of older rocks must represent the remains of an inland sea, perhaps formerly continuous with the Aral-Caspian basin of Miocene times. The whole recent history of this area would appear to be one of shift from marine to brackish to lacustrine to riverine conditions. Following this has been the sustained recent desiccation of central India in historic times (Sálim Ali, 1927:833-861). Seventeenth century records show the range of the great Indian rhinoceros for example as occurring up to Peshawar and the foothills of the northwest in what is now a semi-desert area.

In view of the above it seems very likely that certain animals adapted for life in or about large bodies of water if capable of the necessary evolutionary modifications, would have been able to adjust to this radical change in environment and continue to persist. Of the four endemic species of Indian birds discussed by Ripley (1961: xxiii) two are endemic Indian genera whose normal habitat is aquatic or semi-aquatic. One is the bristled grass warbler, *Chaetornis*, a bird of the Gangetic drainage system, local in habitat, found in moist grassy places. The other is the Pink-headed Duck, which has been found only in lakes or ponds in the arc from Bihar to eastern Assam, although there are scattered records of nearly a hundred years ago indicating a wider distribution throughout the Indian plains and spottily into the Peninsula. If this species indeed shows affinities with the estuarine diving ducks as we believe the anatomical evidence suggests, then it would appear to be descended from a form which was plastic enough to respond adaptively to long-term changes in the ecology of southern Asia. It evolved gradually into a fresh water surface feeding type of duck as the total water area diminished. Again, with the

disintegration of the Aral-Caspian, it became isolated in the furthest reaches of the increasingly dessicated Gangetic system. The Pink-headed Duck ultimately became trapped, so to speak, in the evironment to which it had become adapted and as a sedentary relict species appears at present to have vanished almost, if not completely, from the scene.

The evolution of the Pink-headed Duck appears to have been related to the major environmental changes which took place in India during Tertiary times. The principal occurrence in the history of this peculiar genus was the development of dabbling-duck-like locomotor adaptations, at least so we infer from the curious modifications of the foot. The trachea, plumage pattern and certain characteristics of the foot leave no doubt about the aythyine relationships of *Rhodonessa*.

Literature Cited

Ali, Sálim, 1927. The Moghul Emperors of India as Naturalists and Sportsmen. Jour. Bombay Nat. Hist. Soc., 31:833-861.

Delacour, Jean, 1956. The Waterfowl of the World, Vol. 2. Country Life Limited. London.

Delacour, Jean, and Ernst Mayr, 1945. The Family Anatidae. Wilson Bull., 57:3-55.

Finn, Frank, 1909. The Water Fowl of India and Asia. Thacker, Spink and Co., Calcutta. ix + 121 p.

Finn, Frank, 1915. Indian Sporting Birds. F. Edwards, London. xi + 280 p.

Garrod, Alfred Henry 1875. On the Form of the Lower Larynx in Certain Species of Ducks. Proc. Zool. Soc. London, 1875:151-156.

Gignoux, Maurice, 1955. Stratigraphic Geology. W. H. Freeman, San Francisco. xvi + 682 p.

Hume, A. O., and C. H. T. Marshall, 1881. The Game Birds of India, Burmah, and Ceylon, Vol. 3. Calcutta.

Humphrey, Philip S., 1955. The Relationships of the Sea Ducks (Tribe Mergini). Ph.D. Dissertation, Univ. Mich.

Johnsgard, Paul A., 1961. The Taxonomy of the Anatidae—A Behavioural Analysis. Ibis, 103a (1961):71-85.

Miller, Alden H., 1937. Structural Modifications in the Hawaiian Goose (*Nesochen sandvicensis*), a Study in Adaptive Evolution. Univ. Calif. Publ. Zool., 42:1-80.

Peters, James Lee, 1931. Check-List of Birds of the World, Vol. 1. Harvard Univ. Press, Cambridge.

Phillips, John C., 1922. A Natural History of the Ducks. Vol. 1. Houghton Mifflin. Boston.

Ripley, S. Dillon, 1950. Vanishing and Extinct Bird Species of India. Jour. Bombay Nat. Hist. Soc., 50:902-906.

Ripley, S. Dillon, 1961. A Synopsis of the Birds of India and Pakistan. Bombay Natural History Society.

Salvadori, Tommaso, 1895. Catalogue of the Chenomorphae (Palamedeae, Phoenicopteri, Anseres), Crypturi, and Ratitae in the collection of the British Museum. Catalogue of the birds in the British Museum, Vol. 27. London.

Verheyen, René, 1955. La Systématique des Ansériformes Basée sur l'Ostéologie Comparée (suite). Bull. Inst. Roy. Sci. Nat. Belgique, Vol. 31, no. 37:1-22.

Wadia, D. N., 1944. Geology of India. London.

Woolfenden, Glen E., 1959. A Pleistocene Avifauna from Rock Spring, Florida. Wilson Bull., 71:183-187.

Woolfenden, Glen E., 1961. Postcranial Osteology of the Waterfowl. Bull. Fla. State Mus., Vol. 6, no. 1:1-129.